Agroforest Syst (2009) 76:317–325
DOI 10.1007/s10457-009-9213-2

Soil phosphorus and water effects on growth, nutrient and carbohydrate concentrations, δ^{13}C, and nodulation of mimosa (*Albizia julibrissin* Durz.) on a highly weathered soil

Adrian Ares · David M. Burner · David K. Brauer

Received: 2 November 2007 / Accepted: 19 January 2009 / Published online: 10 February 2009

Abstract Growth and physiological performance of multipurpose tree species can be severely constrained by low phosphorus (P) availability in highly weathered soils. Limitations to plant growth are accentuated by seasonal dry periods. The overall objective of this study was to examine P fertilization and irrigation effects on survival, growth, biomass partitioning, foliar nutrients, intrinsic water-use efficiency (WUE) indexed by δ^{13}C, *Rhizobium* nodulation, and carbohydrate content as an indicator of resprouting potential, of mimosa (*Albizia julibrissin* Durz.), a N_2-fixing tree species being tested for browse in agroforestry practices in south-central USA. In a field experiment carried out during two growing seasons near Booneville, Arkansas, USA, mimosa had a strong growth response to irrigation. The trial was arranged in a split plot design with three replications with irrigation as main plot treatment and P as sub-plot treatment. Mean total plant aboveground biomass at the end of the second growing season was 9.8 and 44.1 g plant^{-1} for the rainfed treatment without and with 300 mm of irrigation water, respectively. Placed P fertilization increased mean total aboveground biomass from 19 g plant^{-1} for the 0-P treatment to 69 g plant^{-1} for the treatment with 90 kg P ha^{-1} year^{-1}. Similarly, irrigation consistently increased stem basal diameter, total height, survival, root, stem, foliar and total aboveground biomass, and number of nodules per plant. Phosphorus fertilization increased basal diameter, and root and stem biomass in both irrigation treatments, survival and nodulation in the rainfed treatment, and foliar and total aboveground biomass in the rainfed +300 mm irrigation treatment. There was a decrease of foliar δ^{13}C suggesting that WUE decreased with P fertilization. In a pot experiment, seedlings were subjected to a factorial combination of two irrigation treatments and six P levels in a randomized complete block design. Irrigation increased basal diameter, root, stem, foliar and total biomass, leaf area and nodulation, whereas P fertilization (i.e., levels from 0 to 3.68 g P kg^{-1} soil) had similar effect in all the above variables except foliar biomass. Foliar P concentration to obtain 90% of the maximum total plant biomass (critical level) was estimated at 0.157%. Total non-structural and water soluble carbohydrate, and starch concentrations increased non-linearly with irrigation and P addition suggesting impaired re-growth potential after defoliation of seedlings with reduced water supply and at low soil P availability. Results of this study indicated strong limitations for growth and regrowth potential of mimosa on a highly weathered soil with very low P availability and seasonal water

A. Ares (✉)
Oregon State University, Corvallis, OR, USA
e-mail: adrian@hawaii.edu

D. M. Burner
ARS-USDA, Booneville, AR, USA

D. K. Brauer
ARS-USDA, Bushland, TX, USA

content shortages. Placed (i.e., near the plant base) application of P appeared to be a good strategy to fertilize perennial woody plants.

Keywords Mimosa · Irrigation · P nutrition · Stable carbon isotopes

Introduction

Growth and development of many tree species are severely limited by nutrient shortages in highly weathered soils. Available soil phosphorus (P) is often very low in soils derived from geologically old substrates in areas such as the southern and central regions of the United States of America. Plant growth is further constrained during seasonal dry periods. Plants may respond to nutrient and water limitations by adjusting nutrient and carbohydrate content (Graham et al. 1997), biomass accumulation and partitioning (Cromer and Jarvis 1990), and resource-use efficiencies (Ares and Fownes 2001). Other responses may include changes in leaf morphology (Castro-Díez et al. 1997), nutrient resorption (Ares and Gleason 2006), phenology (Sigurdsson 2001), and N_2-fixation (Robson et al. 1981).

In this study, we examined growth, resource-use and physiological responses of mimosa (*Albizia julibrissin* Durz.) to irrigation and P fertilization in central-western Arkansas, USA. Mimosa is a N_2-fixing, cold-tolerant tree species native to Asia which has been commonly used in amenity plantations, and for papermaking (Duke et al. 2003), medicinal products (Ekenseair et al. 2006), and fodder because of its high crude protein content (Burner et al. 2007). In the southern USA, mimosa has been considered in agroforestry practices as goat (Addlestone et al. 1998) and cattle browse (Bransby et al. 1992), and for soil fertility improvement in permaculture systems (Matta-Machado and Jordan 1995; Rhoades et al. 1997; Jordan 2004). Planting of mimosa should be evaluated on a site-specific basis because it can become invasive especially in riparian areas (Loewenstein and Loewenstein 2005).

It is not known the extent to which soil water and nutrients limit mimosa growth and survival in marginal arable lands. Low P and seasonally low soil water may reduce biomass production, and impair physiological performance of mimosa. Under limiting growth conditions, tree seedlings may exhibit altered efficiency of resource utilization. Thus, it is important to examine the relative strength of soil water and nutrient limitations. Decreased water supply can increase the ratio between net photosynthesis and stomatal conductance (i.e., intrinsic water use efficiency; Ferrio et al. 2003) often indexed by the stable carbon (C) composition ($\delta^{13}C$) of plant tissues (Ripullone et al. 2004). Thus, $\delta^{13}C$ in plant tissues may be an integrated indicator of water supply reduction (Choi et al. 2005), and be used to infer possible effects of past soil water deficits on plants. Several studies have addressed effects of water stress and N additions on $\delta^{13}C$ (Clay et al. 2001; Lopes et al. 2004; Dercon et al. 2006) but there is limited information for P and water.

The objectives of this study were to determine the responses of mimosa to soil water and P additions in terms of (1) survival (SUR), (2) plant size, (3) biomass partitioning, (4) leaf area and morphology, (5) intrinsic water-use efficiency, (6) carbohydrate content as an indicator of re-sprouting potential, and (7) *Rhizobium* nodulation. Toward these purposes, a field and an outdoor pot experiment were conducted in central-western Arkansas. In the field experiment, mimosa responses to water and P additions (0 and +) were assessed. In the pot experiment, a range of P additions to the soil allowed to develop biomass and carbohydrate response functions, and derive P foliar critical levels.

Materials and methods

The field experiment was conducted from February 2001 to October 2002 near Booneville, Arkansas, USA (35.11°N, 93.95°W) at about 150 m above sea level. The soil was a silt loam Fragiudult (Soil Survey Staff 1992) of the Leadvale series. At 0–20 cm depth, the soil had pH (1:2 soil:water) 5.3, 3 mg kg^{-1} of initial extractable P, 0.01% K, 0.03% Ca, 0.01% Mg, 10 mg kg^{-1} S, 63 mg kg^{-1} Fe, 63 mg kg^{-1} Mn, 1 mg kg^{-1} Zn and 0.6 mg kg^{-1} Cu (extracted following the Mehlich 3 procedure and determined with inductively coupled plasma emission spectrometry). Total N determined by combustion using a LECO CN-2000 analyzer (LECO Corporation, St Joseph, MI) was 0.15%.

The experimental site received blanket fertilization in a single application of 137 kg ha^{-1} K as potash and 10 kg S as $MgSO_4$, and also 1,800 kg ha^{-1} of $CaCO_3$, and 700 kg ha^{-1} $CaSO_4$ in February 2001 to ameliorate nutrient and soil acidity constrains. The target pH was 6.0–6.5 for the Leadvale soil, and the target soil Ca and S were 0.12% and 12 mg kg^{-1}, respectively. Glyphosate (*N*-phosphono-methyl glycine) herbicide was applied before the start of the experiment. Mimosa seedlings from seed collected in Oklahoma, USA, were grown in dibble tubes, and their roots were inoculated with *Rhizobium* strains (Liphatech, Milwaukee, WI, USA). Seedlings were shovel-planted in March 19, 2001 at a spacing of 0.5 m × 0.5 m. All plants were irrigated for several weeks for proper establishment. Every plot contained 16 plants of which measurements were taken from the interior four plants, unless otherwise noted. Plot borders were 4 m apart.

Seedlings were subjected to a factorial combination of two P-fertilization treatments (0 and 90 kg P $year^{-1}$) and two water- supply regimes. The P rate was chosen with the intention to raise available soil P to 100 mg kg^{-1} following the P sorption function for the Leadvale soil (D. Brauer, personal communication, 2001). Phosphorus was applied as triple super phosphate placed at approximately 15-cm soil depth and 20 cm distance from the seedlings in March 2001. The P application was repeated in March 2002. Water supply regimes were rain-fed, and rain-fed plus sprinkler irrigation three times a week from June to October accounting for an additional 300 mm $year^{-1}$ to keep soil water contents near field capacity. Water for irrigation was pumped from a nearby pond. The trial was arranged in a split plot design with three replications with irrigation as main plot treatment and P as sub-plot treatment. Volumetric soil water content was measured weekly from April to October of 2001 and 2002 at 10- and 35-cm depth with a Trime@-time domain reflectrometry (TDR) probe (MESA Systems Co., Medfield, MA, USA) in one irrigated and one non-irrigated plot per block (6 probes in total).

Height and basal diameter of mimosa seedlings were measured in November 2001 and before harvest in October 2002. Aboveground plant biomass was harvested in October 2002 and separated into stem and foliage components. Plant portions were then dried at 70°C until constant weight. Foliar samples (including the entire bipinnately compound leaves) were composited by pooling equal-mass subsamples for each plot. Foliar N was determined by combustion in a LECO FP428 analyzer. Phosphorus, K, Ca, Mg, S, Fe, Mn, Zn, and Cu were analyzed by inductively coupled plasma spectroscopy. Root systems of two randomly selected plants per plot were excavated at harvest to 1-m depths, and number of nodules per plant (NOD) was counted. Fine roots were recovered by sieving the soil with a 0.5-mm sieve. Root biomass (RB) was recorded after roots were dried at 70°C until constant weight. Dried foliar and root (including both fine and coarse roots) samples were finely reground, and analyzed for $\delta^{13}C$ at the Environmental Stable Isotope laboratory of Duke University, Durham, NC, USA by using a continuous-flow mass spectrometer Finnigan MAT Delta Plus XL (Finnigan MAT, Bremen, Germany). For leaves, 36 samples were analyzed for $\delta^{13}C$ (three plants per plot × two irrigation regimes × two P addition treatments × three blocks). For roots, 12 samples were analyzed for $\delta^{13}C$ (one composite sample per plot × two irrigation regimes × two P addition treatment × three blocks). Replicated samples sent to test the repeatability of the $\delta^{13}C$ values were very close (< 0.01% difference).

A complementary outdoor plot experiment was carried out from July 30, 2002 to October 10, 2002. Mimosa seedlings of similar size were transplanted to 4.8-l pots filled with 80% Leadvale topsoil and 20% perlite. The soil received the same amendments as the field experiment. Seedlings were subjected to a factorial combination of two irrigation treatments (2.1 and 10.4 mm water day^{-1}) and six P levels (0, 0.23, 0.46, 0.92, 1.84, and 3.68 g P kg^{-1} soil) with P applied as triple super phosphate, in a randomized complete block design with six replicates.

At harvest, roots, foliage and stems were separated, and subsamples composited by plant were placed in storage at −20°C for carbohydrate analysis. Starch, total non-structural carbohydrates and water soluble carbohydrates were analyzed as described previously (Denison et al. 1990). Foliar nutrients were determined as in the field experiment for 18 randomly selected plants. Leaf area was measured with a Li-Cor LI-300A area meter (Li-Cor, Lincoln, NE, USA). Leaf mass per unit leaf area, leaf area: plant biomass ratio, and root:shoot biomass ratio were recorded for each harvested plant.

Weather data used to characterize the precipitation and air temperature conditions during both the field and pot experiment were from Booneville, AR. The weather station is at approximately 7 km east of the study site (National Oceanic, Atmospheric Administration 2001, 2002).

Statistical analysis

For the field experiment, irrigation and P addition effects on response variables were examined as a split-plot mixed model (Littell et al. 1996) with irrigation and P addition considered as fixed effects and block as random effect. For the pot experiment, we used a mixed model for a randomized complete block design. The relationship between foliar P concentration and TB was tested using segmented linear regression (Ryan and Porth 2007). Simple rectangular hyperbola functions were fitted to relate root carbohydrates with P supply.

Results

Precipitation, air temperature and soil water content

For the field experiment, precipitation during the April to October growing season was 696 mm in 2001 and 720 mm in 2002. Mean air temperature was 10.8°C in 2001 and 11.1°C in 2002. Volumetric soil water content during the growing season (April to October) at the 10-cm depth averaged 22.8 mm^{-3} ± 1.5 in 2001, and 24.7 mm^{-3} ± 0.9 in 2002 in the irrigation treatment, and 18.4 mm^{-3} ± 1.6 in 2001 and 19.3 mm^{-3} ± 1.2 in 2002 in the non-irrigation treatment. At the 35-cm depth, volumetric water content in the irrigation treatment was 29.7 mm^{-3} ± 1.8 in 2001 and 30.6 mm^{-3} ± 0.6 in 2002, and 25.0 mm^{-3} ± 1.6 in 2001 and 23.1 mm^{-3} ± 0.4 in 2002 in the non-irrigation treatment. For the duration of the pot experiment in 2002, precipitation was 230 mm and mean air temperature was 22.2°C.

Field experiment

At the end of the first growing season, mimosa seedlings subjected to irrigation had already greater height and basal diameter ($P < 0.001$ for both variables) than seedlings without irrigation. Phosphorus fertilization increased basal diameter ($P = 0.06$) but not height ($P = 0.48$).

At the end of the second growing season, total aboveground biomass was on average 9.8 g $plant^{-1}$ for the rainfed treatment and 44.1 g $plant^{-1}$ for the rainfed treatment plus 300 mm of irrigation water. Fertilization with P also increased mean total aboveground biomass from 19 g $plant^{-1}$ for the 0-P treatment to 69 g $plant^{-1}$ in the 90 kg P $year^{-1}$ treatment. At harvest, irrigation consistently increased survival ($P = 0.03$), root, stem and foliar biomass ($P = 0.02$, 0.001 and 0.0001, respectively), and total aboveground biomass ($P < 0.001$; Table 1). Phosphorus addition increased root biomass ($P = 0.06$) and shoot biomass ($P < 0.001$) in both irrigation treatments, survival ($P = 0.04$) and number of nodules per plant ($P = 0.02$) in the rainfed treatment, and foliar biomass ($P < 0.001$) and total aboveground biomass ($P < 0.001$) in the rainfed + 300 mm irrigation treatment. The interaction of irrigation and P fertilization had a significant effect on stem, foliar and total biomass ($P < 0.001$ for all

Table 1 Mean tree survival, biomass, biomass and nodule count of eighteen-month old *Albizia julibrissim* seedlings subjected to irrigation (IRR) and P fertilization in a field experiment in Booneville, USA

IRR mm	Added P kg ha^{-1}	SUR (%)	RB (g $plant^{-1}$)	SB (g $plant^{-1}$)	FB (g $plant^{-1}$)	TAB (g $plant^{-1}$)	NOD (*n* per plant)
0	0	52 ± 16b	25.6 ± 5.1b	5.4 ± 1.5b	3.8 ± 1.0a	9.3 ± 1.8a	80 ± 22b
	180	71 ± 15a	36.3 ± 16.8a	6.3 ± 1.6a	3.7 ± 2.5a	10.0 ± 1.7a	133 ± 50a
300	0	90 ± 10A	133.2 ± 63B	10.0 ± 3.2B	9.2 ± 2.8B	19.2 ± 4.4B	217 ± 58A
	180	92 ± 6A	294.0 ± 82A	37.3 ± 6.2A	31.7 ± 4.4A	69.0 ± 10.0A	212 ± 57A

Values are mean ± one SE of the mean. For a given IRR, means for P addition treatments followed by the same letter do not differ at $P \leq 0.05$. *SUR* survival, *RB* root biomass, *SB* stem biomass, *FB* foliage biomass, *TAB* total aboveground biomass, *NOD* number of nodules per plant

Table 2 Mean root and foliar $\delta^{13}C$ of 18-month *Albizia julibrissim* seedlings subjected to irrigation (IRR) and P fertilization in a field experiment in Booneville, USA

IRR (mm)	Added P (kg ha^{-1})	Foliar $\delta^{13}C$ ‰ ($n = 36$)	Root $\delta^{13}C$ ‰ ($n = 12$)
0	0	−27.6 ± 0.45 a	−28.1 ± 0.31 a
	180	−28.4 ± 0.32 b	−28.8 ± 0.51 a
300	0	−27.2 ± 0.44 A	−27.2 ± 0.37 A
	180	−28.5 ± 0.34 B	−28.4 ± 0.37 A

Values are mean ± one SE of the mean. For a given IRR, mean $\delta^{13}C$ values for P addition treatments followed by the same letter in columns do not differ at $P \leq 0.05$

these interactions) indicating a better effect of P on these variables with irrigation. Number of nodules was positively correlated to root biomass ($r^2 = 0.79$, $P = 0.01$), stem biomass ($r^2 = 0.63$, $P = 0.02$), foliar biomass ($r^2 = 0.66$, $P = 0.02$) and total aboveground biomass ($r^2 = 0.64$, $P = 0.02$).

Irrigation increased foliar Mg concentration (range = 0.15–0.32%) in the 0-P treatment at the final harvest ($P = 0.03$). Phosphorus addition increased foliar concentrations of P (range = 0.12–0.19%) in both irrigation treatments ($P = 0.04$) and Mg (range = 0.28–0.42%) in the rainfed treatment ($P = 0.04$). The interaction of irrigation and P fertilization had a significant effect on foliar Mg concentration ($P = 0.02$). No other foliar nutrients were affected by irrigation or P fertilization. Phosphorus addition decreased leaf $\delta^{13}C$ (i.e., more negative values; $P = 0.02$; Table 2).

Pot experiment

Irrigation increased basal diameter ($P = 0.002$), root biomass ($P < 0.0001$), stem biomass ($P < 0.0001$), foliar biomass ($P = 0.003$), total biomass ($P < 0.0001$), leaf area ($P < 0.0001$), and number of nodules ($P < 0.0001$; Table 3). Phosphorus addition increased basal diameter ($P = 0.05$), root biomass ($P = 0.004$), stem biomass ($P = 0.04$), total biomass ($P = 0.003$), leaf area ($P = 0.01$), and number of nodules ($P = 0.07$). The interaction of irrigation and P was only significant for stem biomass. Irrigation and P addition did not affect specific leaf mass, leaf area ratio and root:shoot ratio (data not shown). Number of nodules per plant was positively correlated to root biomass ($r^2 = 0.67$, $P = 0.001$), stem biomass ($r^2 = 0.55$, $P = 0.01$), foliar biomass ($r^2 = 0.62$, $P = 0.001$) and total aboveground biomass ($r^2 = 0.66$, $P = 0.001$).

Phosphorus addition only increased foliar P content ($P = 0.01$). The leaf P critical level to obtain 90% of the maximum total plant biomass was 0.157% (Fig. 1). We were unable to determine the soil P critical level because of the large data variability but

Table 3 Mean tree basal diameter, height, component and total biomass, leaf area, and nodule count of *Albizia julibrissim* seedlings subjected to irrigation (IRR) and P fertilization in a pot experiment in Booneville, USA

IRR (cm^3 day^{-1})	Added P (g kg^{-1})	BD (mm)	HT (cm)	RB (g $plant^{-1}$)	SB (g $plant^{-1}$)	FB (g $plant^{-1}$)	TB (g $plant^{-1}$)	LA (cm^2 $plant^{-1}$)	NOD (*n* per plant)
2.1	0	4.2 ± 0.5	49.7 ± 2.3	6.6 ± 1.2	2.6 ± 0.5	1.4 ± 0.3	10.5 ± 2.0	216 ± 60	25.0 ± 7
	0.23	3.9 ± 0.4	46.7 ± 3.5	5.2 ± 0.5	2.2 ± 0.5	1.9 ± 0.9	9.3 ± 1.8	255 ± 38	42.3 ± 3
	0.46	4.1 ± 0.2	53.0 ± 5.2	6.7 ± 1.7	2.8 ± 0.7	1.8 ± 0.7	11.1 ± 2.9	305 ± 91	46.0 ± 13
	0.92	3.9 ± 0.4	52.0 ± 3.5	7.6 ± 1.5	2.6 ± 0.5	1.7 ± 0.4	11.8 ± 2.0	349 ± 87	53.0 ± 24
	1.84	4.8 ± 0.4	54.4 ± 2.6	8.0 ± 1.7	2.9 ± 0.6	2.2 ± 0.5	13.1 ± 2.8	377 ± 104	57.3 ± 11
	3.68	4.4 ± 0.2	50.0 ± 4.2	8.9 ± 0.4	2.8 ± 0.4	2.2 ± 0.5	13.9 ± 1.0	301 ± 35	62.7 ± 3
10.4	0	3.9 ± 0.4	49.3 ± 2.0	6.2 ± 2.0	3.4 ± 0.4	1.6 ± 0.7	11.2 ± 2.1	286 ± 79	49.7 ± 12
	0.23	4.4 ± 0.6	42.7 ± 2.2	9.3 ± 0.4	3.6 ± 0.1	2.1 ± 0.1	15.0 ± 0.6	408 ± 60	142.3 ± 43
	0.46	6.2 ± 0.2	55.7 ± 4.2	15.1 ± 1.6	5.6 ± 0.3	3.4 ± 0.4	24.0 ± 2.2	549 ± 126	147.0 ± 37
	0.92	5.5 ± 0.4	48.7 ± 2.8	16.3 ± 1.0	5.8 ± 0.4	3.5 ± 0.5	25.6 ± 1.1	739 ± 65	149.3 ± 44
	1.84	4.6 ± 0.5	51.0 ± 1.5	15.6 ± 4.3	5.8 ± 1.2	3.7 ± 1.0	25.0 ± 6.2	669 ± 137	149.3 ± 45
	3.68	5.4 ± 0.4	55.3 ± 4.1	18.6 ± 2.3	7.2 ± 0.7	4.7 ± 1.1	30.5 ± 2.6	662 ± 77	226.0 ± 76

Values are mean ± one standard error of the mean. *BD* basal diameter; *HT* height, *RB* root biomass, *SB* stem biomass, *FB* foliage biomass, *TB* total biomass, *LA* leaf area, *NOD* number of nodules per plant

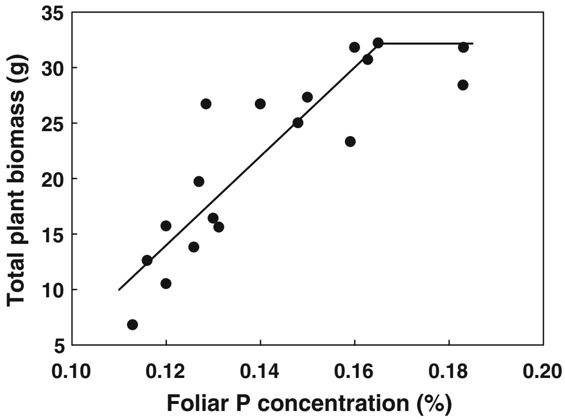

Fig. 1 Total biomass (TB) of *Albizia julibrissim* seedlings in relation to foliar P concentration in a pot experiment in Booneville, AR, USA. TB = −34.12 + 400.95 Foliar P (%) if foliar $P \leq 0.165\%$, TB = 32.2 g if foliar $P > 0.165\%$; R^2_{adj} (for the whole segmented model) = 0.76. Data correspond to the high water supply treatment (10.4 mm water day^{-1})

data suggested that soil P critical level for mimosa in the Leadvale soil could be around 17 mg kg^{-1}.

Root total non-structural and water-soluble carbohydrates, and starch concentrations increased non-linearly with irrigation and P addition ($P < 0.0001$ in all cases; Fig. 2). The interaction of irrigation and P fertilization was significant for total non-structural carbohydrates and starch ($P < 0.001$). Stem carbohydrate concentrations were not affected by irrigation and P addition varying between 8.3 and 12.1% for total-non structural carbohydrates, 1 and 2.3% for water-soluble carbohydrates, and 6.5 and 10.3% for starch.

Discussion

In the field experiment, the response to irrigation was already noticed at the end of the first growing season, whereas response to placed P additions fully developed during the second season. A delayed response in crop growth to P fertilization is often found compared with faster responses for other nutrients such as nitrogen (Weil 2000; Gökkaya et al. 2006). The positive affect of added P on nodulation agreed with previous research showing increased nodule number after P fertilization in N_2-fixing tree species such as *Leucaena* (Sanginga et al. 1991). In addition, to increase P foliar content, P additions appeared to increase Mg uptake of mimosa plants.

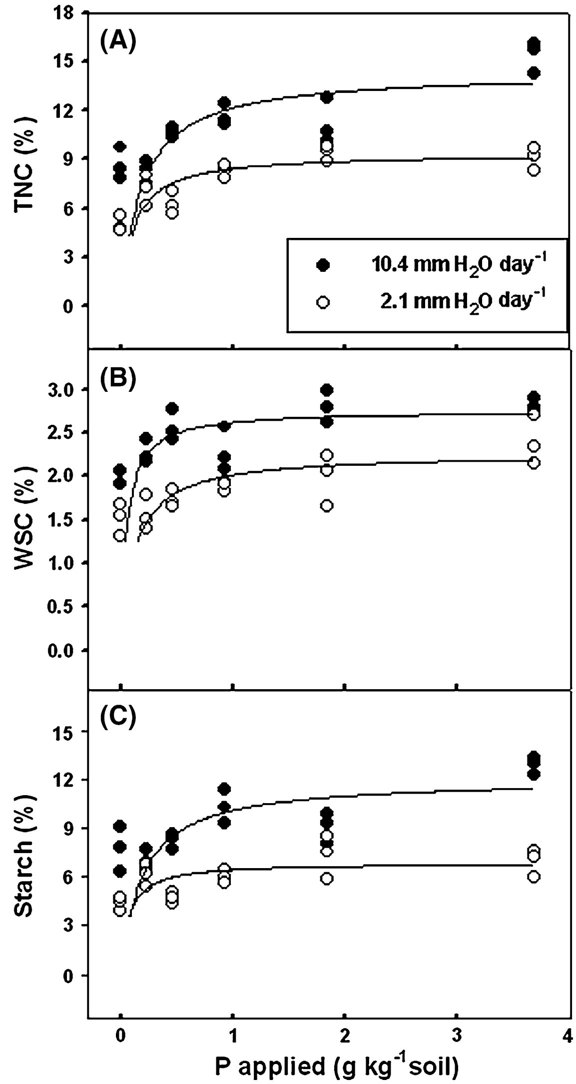

Fig. 2 Total non-structural (TNC, **a**) and water soluble carbohydrate (WSC, **b**), and starch (ST, **c**) concentrations in roots of *Albizia julibrissim* seedlings subjected to irrigation and P additions in a pot experiment in Booneville, AR, USA. Simple *rectangular hyperbola* functions were fitted for both low (LW) and high (HW) water supply to relate carbohydrate concentrations to P added to the soil (P_{added}, g kg^{-1}). TNC (LW) = 9.34 P_{added}/(0.11 + P_{added}), Percent explained variance (PEV) = 95.8; TNC (HW) = 14.34 P_{added}/(0.18 + P_{added}), PEV = 94.5; WSC (LW) = 2.26 P_{added}/(0.12 + P_{added}), PEV = 93.9; WSC(HW) = 2.75 P_{added}/(0.05 + P_{added}), PEV = 94.6; ST (LW) = 6.88 P_{added}/(0.07 + P_{added}), PEV = 92.3; ST (HW) = 12.02 P_{added}/(0.19 + P_{added}), PEV = 93.3

Phosphorus addition appeared to decrease intrinsic water-use efficiency in both irrigation treatments as indicated by decreased leaf $\delta^{13}C$ although there were no significant differences for root $\delta^{13}C$ for which fewer samples were analyzed. The similar trends in $\delta^{13}C$ in leaf and roots indicated that in these young plants the same source of assimilated C constituted both aboveground and belowground tissues. Given the lack of CO_2 assimilation and stomatal conductance measurements in this study, it is difficult to suggest potential causes for the decrease in intrinsic-water use efficiency with P additions. Enhanced P nutrition has been found to increase net CO_2 assimilation rates in tree species (Ben Brahin et al. 1996; Loustau et al. 1999), although no relationships (Conroy et al. 1990; Warren and Adams 2002) or even a negative one (Mulligan 1989) have been determined. In a study with four rainforest tree species, increased foliar P increased net CO_2 assimilation in the subcanopy tree *Quintinia acutifolia* Kirk, but there was no P effect on the other species (Tissue et al. 2005). In this study, it was unlikely that photosynthesis of mimosa plants would have decreased in response to P additions given the strong positive growth response. One possible explanation for the results from the field study is that stomatal conductance increased proportionately more than photosynthesis, leading to higher rates of transpiration. Higher transpirations rates and lower intrinsic WUE could have been also caused by increased root hydraulic conductivity in the P fertilization treatment.

In the pot experiment, there were also positive responses to irrigation and P additions. Phosphorus addition increased foliar P and a foliar P critical level of 0.157% was derived. Irrigation and P addition did not affect specific leaf mass similar to findings for *Pinus pinaster* (Ben Brahin et al. 1996) although specific leaf mass increased in *Eucalyptus grandis* (Kirschbaum et al. 1992). Also P addition did not increase root:shoot ratio contrary to findings for *Pinus serotina* (Topa and Cheeseman 1992).

It is generally accepted that plant carbohydrates are utilized to initiate growth after a dormant period or defoliation (Ball et al. 1991; Gleason and Ares 2004). The strong effect of irrigation and P on root carbohydrates suggested that regrowth potential of mimosa after browsing would be impaired in plants with reduced water supply and soil P. Concentrations of carbohydrates increased sharply at relatively low levels of applied P (i.e., 1 g kg^{-1} soil) to a soil with very low P availability and further increases in applied P had little if any affect on carbohydrate levels. Root carbohydrate concentration has been shown to increase to a maximum level with increasing P supply and then to decrease at saturating P concentrations (Amijee et al. 1990).

The results of this study indicated strong limitations for growth and regrowth potential of a multipurpose tree such as mimosa on a highly weathered soil with very low P availability and seasonal water content shortages. Placed (i.e., near the plant base) application of P appeared to be a good strategy to fertilize perennial woody plants. Given the limitations for mimosa in central-western Arkansas, native woody species such as black locust may be a better alternative for browsing in agroforestry practices (Burner et al. 2005).

Acknowledgments The Agricultural Research Service-United States Department of Agriculture funded this investigation. We are grateful to Karen Chapman, Tammy Horton, Jimmy Whiley and Brent Woolley for valuable technical assistance, and David Belesky and Joyce Ruckle for carbohydrate analyses.

References

Addlestone BJ, Mueller JP, Luginbuhl PM (1998) The establishment and early growth of three leguminous tree species for use in silvopastoral systems in the southern USA. Agrofor Syst 44:253–265. doi:10.1023/A:1006254812236

Amijee F, Stribley DP, Tinker PB (1990) Soluble carbohydrates in roots of leek *Allium porrum* plants in relation to phosphorus supply and VA mycorrhizas. Plant Soil 124:195–198. doi:10.1007/BF00009259

Ares A, Fownes JH (2001) Productivity, resource use and competitive interactions of *Fraxinus uhdei* in Hawaii uplands. Can J For Res 31:1–11. doi:10.1139/cjfr-31-1-132

Ares A, Gleason SM (2006) Foliar nutrient resorption in tree species. In: Parks AP (ed) New research on forest ecology. Nova Science Publishers, Hauppauge, pp 1–33

Ball DM, Hoveland CS, Lacefield GD (1991) Southern forages, 1st edn. Potash & Phosphate Institute, Atlanta 256 pp

Ben Brahin M, Loustau D, Gaudillere JP, Saur E (1996) Effects of phosphate deficiency on photosynthesis and accumulation of starch and soluble sugars in 1-year-old seedlings of maritime pine (*Pinus pinaster*). Ann Sci For 53:801–810. doi:10.1051/forest:19960401

Bransby DI, Sladden SE, Aiken GE (1992) Mimosa as a forage plant: a preliminary evaluation. Proceeding Forage Grassland Conference, Georgetown, TX, USA. Am Forage Grassl Counc 1:28–31

Burner DM, Pote DH, Ares A (2005) Management effects on biomass and foliar nutritive value of *Robinia pseudoacacia* and *Gleditsia triacanthos* f. inermis in Arkansas, USA. Agrofor Syst 65:207–214. doi:10.1007/s10457-005-0923-9

Burner DM, Carrier DJ, Belesky DP, Pote DH, Ares A, Clausen EC (2007) Yield components and nutritive value of *Robinia pseudoacacia* and *Albizia julibrissin* in Arkansas, USA. Agrofor Syst 72:51–62. doi:10.1007/s10457-007-9098-x

Castro-Díez P, Villar-Salvador P, Pérez-Rontomé C, Maestro-Martínez M, Montserrat Martí G (1997) Leaf morphology and leaf chemical composition in three *Quercus* (Fagaceae) species along a rainfall gradient in NE Spain. Trees-Struct Funct 11:127–134

Choi WJ, Chang SX, Allen HL, Kelting DL, Ro HM (2005) Irrigation and fertilization effects on foliar and soil carbon and nitrogen isotope ratios in a loblolly pine stand. For Ecol Manage 213:90–101. doi:10.1016/j.foreco.2005.03.016

Clay DE, Engel RE, Long DS, Liu Z (2001) Nitrogen and water stress interact to influence Carbon-13 discrimination in wheat. Soil Sci Soc Am J 65:1823–1828

Conroy JP, Milham PJ, Reed ML, Barlow EWR (1990) Increases in phosphorus requirements for CO_2-enriched pine species. Plant Physiol 92:977–982. doi:10.1104/pp.92.4.977

Cromer RN, Jarvis PG (1990) Growth and biomass partitioning in *Eucalyptus grandis* seedlings in response to nitrogen supply. Aust J Plant Physiol 17:503–515

Denison RF, Fedders JM, Ong CBS (1990) Amyloglucosidase hydrolysis can overestimate starch concentration of plants. Agron J 82:869–873

Dercon G, Clymans E, Diels J, Merckx R, Deckers J (2006) Differential ^{13}C isotopic discrimination in maize at varying water stress and at low to high nitrogen availability. Plant Soil 282:313–326. doi:10.1007/s11104-006-0001-8

Duke SR, Reed PJ, Hanjie G, Krishnagopalan G, Morrison TA, Bransby DI (2003) Potential of mimosa (*Albizia julibrissin*) for papermaking. TAPPI 2:9–12

Ekenseair AK, Duan L, Carrier DJ, Bransby DI, Clausen EC (2006) Extraction of hyperoside and quercitrin from mimosa (*Albizia julibrissin*) foliage. Appl Biochem Biotechnol 130:382–391. doi:10.1385/ABAB:130:1:382

Ferrio JP, Florit A, Vega A, Serrano L, Voltas J (2003) $\delta^{13}C$ and tree-ring width reflect different drought responses in *Quercus ilex* and *Pinus halepensis*. Oecologia 137:512–518. doi:10.1007/s00442-003-1372-7

Gleason SM, Ares A (2004) Ecophysiology of native and invasive tree species: growth, photosynthesis, and carbohydrate storage of koa and tropical ash in relation to light and defoliation. Tree Physiol 24:1087–1097

Gökkaya K, Hurd TM, Raynal DJ (2006) Symbiont nitrogenase, alder growth, and soil nitrate response to phosphorus addition in alder (*Alnus incana* ssp. rugosa) wetlands of the Adirondack Mountains, New York State, USA. Environ Exp Bot 55:97–109. doi:10.1016/j.envexpbot.2004.10.004

Graham JH, Duncan LW, Eissenstat DM (1997) Carbohydrate allocation patterns in citrus genotypes as affected by phosphorus nutrition, mycorrhizal colonization and mycorrhizal dependency. New Phytol 135:335–343. doi:10.1046/j.1469-8137.1997.00636.x

Jordan CF (2004) Organic farming and agroforestry: alleycropping for mulch production for organic farms in southern United States. Agrofor Syst 61–62:79–90. doi:10.1023/B:AGFO.0000028991.86647.35

Littell RC, Milliken GA, Stroup WW, Wolfinger RD (1996) SAS system for mixed models. SAS Institute Inc., Cary

Loewenstein NJ, Loewenstein EK (2005) Non-native plants in the understory of riparian forests across land use gradient in the Southeast. Urban Ecosyst 8:79–91. doi:10.1007/s11252-005-1420-7

Lopes MS, Nogues S, Araus J (2004) Nitrogen source and water regime effects on barley photosynthesis and isotope signature. Funct Plant Biol 31:995–1003. doi:10.1071/FP04031

Loustau D, Brahim MB, Gaudillère JP, Dreyer E (1999) Photosynthetic responses to phosphorus nutrition in 2-year-old maritime pine seedlings. Tree Physiol 19:707–715

Matta-Machado RP, Jordan CF (1995) Nutrient dynamics during the first three years of an alleycropping agroecosystem in southern USA. Agrofor Syst 30:351–362. doi:10.1007/BF00705219

Mulligan DR (1989) Leaf phosphorus and nitrogen concentrations and net photosynthesis in *Eucalyptus* seedlings. Tree Physiol 5:149–157

National Oceanic, Atmospheric Administration (NOAA) (2001) Climatography of the United States No. 81, Arkansas. NOAA, National Climatic Data Center, Asheville

National Oceanic, Atmospheric Administration (NOAA) (2002) Climatography of the United States No. 81, Arkansas. NOAA, National Climatic Data Center, Asheville

Rhoades CC, Nissen TM, Kettler JS (1997) Soil nitrogen dynamics in alley cropping and no-till systems on ultisols of the Georgia Piedmont, USA. Agrofor Syst 39:31–44. doi:10.1023/A:1005995201216

Ripullone F, Lauteri M, Grassi G, Amato M, Borghetti M (2004) Variation in nitrogen supply changes water-use efficiency of *Pseudotsuga menziesii* and *Populus x euroamericana*: a comparison of three approaches to determine water-use efficiency. Tree Physiol 24:671–679

Robson AD, O'Hara GW, Abbott LK (1981) Involvement of phosphorus in N fixation by subterraenum clover (*Trifolium subterraneum* L.). Aust J Plant Physiol 8:427–436

Ryan SE, Porth LS (2007) A tutorial on the piecewise regression approach applied to bedload transport data. USFS Gen. Tech. Rep. RMRS-GTR-189. Fort Collins, CO, USA, 41 p

Sanginga N, Bowen GD, Danso SKA (1991) Intra-specific variation in growth and P accumulation of *Leucaena leucocephala* and *Gliricidia sepium* as influenced by soil phosphate status. Plant Soil 133:210–218. doi:10.1007/BF00009192

Sigurdsson BD (2001) Elevated CO_2 and nutrient status modified leaf phenology and growth rhythm of young *Populus* *trichocarpa* trees in a 3-year field study. Tree Struct Funct 15:403–413

Soil Survey Staff (1992) Keys to soil taxonomy, 5th edn. Pocahontas Press, Inc., Blacksburg SMSS Tech. Monogr. No. 19

Tissue DT, Griffin KL, Turnbul MH, Whitehead D (2005) Stomatal and non-stomatal limitations to photosynthesis in four tree species in a temperate rainforest dominated by *Dacrydium cupressinum* in New Zealand. Tree Physiol 25:447–456

Topa MA, Cheeseman JM (1992) Carbon and phosphorus partitioning in *Pinus serotina* seedlings growing under hypoxic and low-phosphorus conditions. Tree Physiol 10:195–207

Warren CR, Adams MA (2002) Phosphorus affects growth and partitioning of nitrogen to Rubisco in *Pinus pinaster*. Tree Physiol 22:11–19

Weil RR (2000) Soil and plant influences on crop response to two African phosphate rocks. Agron J 92:1167–1175